

# NEMOURIA

*Occasional Papers of the Delaware Museum of Natural History*

NUMBER 25

OCTOBER 30, 1980

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## THE EXTENT AND SEQUENCE OF THE MOLTS OF THE YELLOW-RUMPED WARBLER

*John P. Hubbard\**

### INTRODUCTION

The Yellow-rumped Warbler (*Dendroica coronata*) is a breeding species of northern and western North America, ranging as such from Alaska to Guatemala. This study was undertaken as part of an investigation of the overall relationships and evolution of this complex of variously differentiated populations (see Hubbard 1967, 1969, 1970), and it focuses on the descriptive aspects of the molts. Aside from Foster's study (1967) of the Orange-crowned Warbler (*Vermivora celata*), I know of no detailed work that has been published on the molts of a member of the family Parulidae occurring over such an extended range. Treated here are all the races of *D. coronata*, that is, *D. c. coronata* (includes *D. c. hooveri*), breeding in northern North America; *D. c. auduboni* (includes *D. c. memorabilis*), breeding in western United States and adjacent Canada; *D. c. nigrifrons*, apparently resident in northwestern Mexico; and *D. c. goldmani*, resident in Guatemala and adjacent Mexico.

The molts of *D. c. coronata* have been treated by Dwight (1900), whereas those of *D. c. auduboni* are covered in a general way in Bent (1953), Swarth (1926), and Phillips et al. (1964). The molts of *D. c. nigrifrons* and *D. c. goldmani* are not treated in the literature, and they appear not to have been previously studied. In general, the extent and sequence of molt among the various races are closely similar, with the exceptions being pointed out in the discussions that follow.

### MATERIALS AND METHODS

I examined almost 2000 specimens for molt, including 68 of the rare *D. c. nigrifrons* and 26 *D. c. goldmani*. Of these, 246 in active molt were selected to document the extent and sequence of molts in this complex. These included 110

*coronata*, 120 *auduboni*, and 16 *nigrifrons*, with 43 in postjuvenal (or first prebasic) molt, 95 in prenuptial (or prealternate) molt, and 108 in postnuptial (or prebasic) molt. No specimens were available of birds in the postnatal molt; hence, it is not discussed in this paper.

The selected specimens were examined under a high-intensity Tensor lamp with a 60 watt bulb, and most were viewed under magnification. Feathers were gently probed with a dissecting needle, and detailed comparisons and notes were made on each of the specimens. Many other molting specimens were examined in a more superficial manner, mainly to check the documented data and to provide other insights into molt. Examined in this manner were several hundred additional specimens, especially those in the postjuvenal and postnuptial molts.

In order to facilitate comparisons with the molts of *Vermivora celata*, the nomenclature used for feather tracts in this paper follows Foster (1967). Primaries are numbered from the inside out, with the outermost (vestigial) primary being number 10. Secondaries are numbered from the outside in, with the innermost (tertials) being 7, 8, and 9.

#### Postjuvenal Molt

The postjuvenal body molt generally begins between the time the tail is one-quarter and one-half grown. As a rule it initially involves the upper and lower marginal wing coverts and often the crural tract (Table 1). Molt then starts in the anterior humeral tract and, either simultaneously or slightly later, in the adjacent sternal region of the ventral tract. As the tail nears full length, additional loci appear on the forehead, chin, and/or throat, and in the pelvic portion of the dorsal tract, the latter giving rise to the yellow rump. Also at this time or slightly later, molt begins in the femoral tract and in the cervical region of the ventral tract. The spread and anastomosing of the ventral molt loci progressively give rise to the inverted-Y pattern of new feather growth characteristic of the ventral area in the juveniles of many passerines. Additional molt then appears on the posterior capital tract and dorsal region of the spinal tract; and the replacement of the greater and, later, the middle secondary coverts begins. Molt finally spreads from established loci to the sides of the head, the spinal cervical region, abdominal region, and tail coverts; and these are among the last areas to acquire the winter plumage. Retained at this molt are the remiges, rectrices, primary coverts, and alular feathers. The statement in Phillips et al. (1964:151) that this molt ("prebasic") is complete in young birds refers to the body plumage only (A. R. Phillips, pers. comm.).

#### Postnuptial Molt

Generally, the replacement of body plumage in this molt begins at the time of the loss of the first or second primary (Table 2). Simultaneously or closely following this loss is initial molt in the anterior marginal coverts, although in a

TABLE 1: The Sequence of Inception of the Postjuvenile Molt

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1. Alar tract (marginal coverts)  
Crural tract
  2. Humeral tract (anterior)  
Ventral tract (sternal region)
  3. Capital tract (frontal, malar regions)  
Ventral tract (cervical, interramal, submalar, axillary regions)  
Spinal tract (pelvic region)  
Femoral tract
  4. Capital tract (coronal, loral, occipital regions)  
Spinal tract (dorsal, interscapular regions)  
Alar tract (greater secondary coverts)
  5. Capital tract (auricular, superciliary regions)  
Ventral tract (abdominal region)  
Spinal tract (cervical region)  
Alar tract (middle secondary coverts)  
Caudal tract (tail coverts)
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TABLE 2: The Sequence of Inception of the Postnuptial Molt

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1. Alar tract (primaries 1, 2; marginal coverts)
  2. Alar tract (primary 3; secondary 8)  
Caudal tract (rectrices 1, 2\*, 3\*; tail coverts)  
Spinal tract (pelvic region)  
Femoral tract
  3. Alar tract (primary 4)  
Spinal tract (pelvic region)  
Femoral tract  
Humeral tract (anterior)
  4. Alar tract (primary 5; secondary 9; greater secondary coverts)  
Caudal tract (rectrices 4, 5\*, 6\*)  
Ventral tract (cervical region)  
Crural tract
  5. Alar tract (primary 6; secondaries 1\*, 7\*)  
Spinal tract (interscapular region)  
Ventral tract (interramal, submalar regions)  
Capital tract (occipital, malar regions)
  6. Alar tract (primary 7; middle secondary coverts)  
Ventral tract (abdominal region)
  7. Alar tract (primary 8; secondaries 2, 3\*, 4\*)  
Spinal tract (cervical region)  
Capital tract (coronal, frontal, loral, superciliary, auricular regions)
  8. Alar tract (primaries 9, 10; secondaries 3, 4\*, 6\*, 5\*)
  9. Alar tract (alular feathers)
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\* May be affected somewhat later.

few cases I have not been able to detect molt there as late as the loss of the third or (very rarely) fourth primary. The first sign of body molt is usually in the pelvic region (rump) of the spinal tract; this is followed by the femoral tract, generally coinciding with the loss of the third or fourth primaries. Also with the loss of the third primary is that of the eighth secondary (middle tertial) and first to third pairs of rectrices; molt of the tail coverts usually also begins at this time. Generally with the loss of the fourth primary, additional loci appear in the sternal region of the ventral tract and in the humeral tract; molt then moves anteriorly from the pelvic to the dorsal region of the spinal tract. As the fifth primary is dropped, usually the ninth secondary is also lost, and molt begins in the crural region. At the same time, molt in the ventral tract moves from the sternal region to the cervical region. Often by this time many birds have lost all, or all but the outer pair or two, of the old rectrices. With the loss of the sixth primary, molt generally begins on the head—especially on the chin, throat, and the lateral and posterior occipital areas. At the same time in the spinal tract, molt spreads anteriorly into the interscapular region. With the loss of this primary or the seventh, the first and seventh secondaries are also dropped, as well as the last of any remaining old rectrices. Rectrix growth is rapid, and the tail is usually nearly full grown before the seventh primary reaches its full length. Starting with the loss of the eighth primary, the remaining secondaries are gradually dropped in the order 2-3-4-6-5. With the molting of the eighth, ninth, and vestigial (tenth) primaries, molt begins on the forehead, auriculars, middle of the crown, and cervical region of the spinal tract. These areas, along with the chin and the abdomen, are generally the last in which body molt is completed.

The greater secondary coverts are generally lost with the dropping of the fifth or sixth primaries, and the middle ones are lost after the greater coverts are partially erupted—usually by the time the eighth primary has been dropped. The primary coverts fall in sequence with their attendant primaries, the first new ones usually not appearing before the fourth primary is dropped. The alular feathers are the last of the wing to be replaced. In the final stages of remix growth, the outer primaries and the inner secondaries reach full growth nearly simultaneously.

Although the power of flight is retained during the course of this molt, there is a reduction in the wing area that probably inhibits flight to a degree. Some estimate of this reduction can be made by calculating the percent that each of the major remiges (excluding the tiny tenth primary and ninth secondary) contributes to the wing area, and then summing the areal reduction in specimens at different stages of molt. Thus, one finds that primaries 5, 6, and 7 each comprise about 7 percent of the wing area; primaries 1, 2, and 3 and secondaries 4, 5, 6, 7, and 8 are each 5 percent, and the remaining remiges 6 percent. In 47 heavily molting specimens, the maximum reduction in wing area ranged from 10 to 30 percent, with the median 20 percent. The reduction of wing area with the loss of given remiges varies considerably because of slightly different rates of replace-

ment of other remiges; however, the greatest reduction is generally at the time of loss of primaries 7, 7+8, and 8+9. Large reductions of wing area (25 to 30 percent) also occurred with the loss of primaries 3+4, 4+5, 5+6, and 6; but generally the loss of single or pairs of primaries in this range caused lesser reductions (10 to 25 percent). Assuming that the loss of wing area reduces flight capacity and makes molting individuals more vulnerable to predation, one can appreciate the increased secretiveness reported in many passerines during their postnuptial molt.

### Prenuptial Molt

Generally, the prenuptial molt begins on the upper midback and the middle and upper breast (Table 3). This is usually followed by molt beginning first on the sides of the anterior part of the crown and then on the lores and forehead. At this time, replacement of the greater and middle secondary coverts begins, and this aspect of molt produces the characteristic wing covert patterns of the various subspecies. Usually the inner five or six pairs of coverts are renewed, whereas the distal three or four pairs are retained. With the beginning of molt on the throat, the loci elsewhere show progression anteriorly and posteriorly. In the final stages, molt includes the feathers of the chin, central crown, auriculars, nape, and anterior scapulars. Generally retained at this molt, in addition to the flight feathers, are most of the wing coverts, the tail coverts, the lower scapulars, and the feathers of the rump and abdomen. In females the molt is often less extensive than in males, with some specimens showing very few, if any, signs of a prenuptial molt. However, in most females, there is at least a partial replacement of the dorsal and ventral body plumage, particularly on the head, back, and breast.

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TABLE 3. The Sequence of Inception of the Prenuptial Molt

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1. Spinal tract (interscapular region)  
Ventral tract (cervical, sternal regions)
  2. Spinal tract (dorsal, cervical regions)  
Capital tract (frontal region)
  3. Ventral tract (submalar region)  
Capital tract (loral, malar regions)  
Humeral tract (anterior)  
Alar tract (greater and middle secondary coverts)
  4. Ventral tract (interramal region)  
Capital tract (coronal, auricular, superciliary, occipital regions)  
Humeral tract (anterior scapulars)
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## DISCUSSION

Comparison of Molts within *Dendroica coronata*

The postnuptial, postjuvenile, and prenuptial molts differ from one another both in the extent of plumage replacement and in the sequence with which feather tracts are affected. In the relative extent of plumage replacement, the molts may be ranked as follows: postnuptial, postjuvenile, and prenuptial.

The postnuptial molt replaces all of the plumage, whereas the postjuvenile replaces all except the remiges, rectrices, primary coverts, and alular feathers. The prenuptial molt replaces a more variable amount of plumage, depending on sex and possibly age and subspecies. In males of *coronata* and *auduboni*, most of the body plumage is replaced (but usually not on the rump, tail coverts, and abdomen), whereas on the wings only the inner five or six pairs of greater and middle secondary coverts are renewed.

The extent of the molt in males of the races *nigrifrons* and *goldmani* is less certain, mainly because of the absence of sufficient specimen material. It is clear that first-year males of both races undergo an extensive prenuptial molt, because their femalelike winter plumage differs from their breeding plumage; thus, the latter can hardly be assumed by wear alone. On the other hand, adult males of *goldmani* appear to be identical in winter and breeding seasons, and it is conceivable that they do not have a prenuptial molt. The only "summer" adult male of this race I have seen is from early May. The plumage wear in this specimen is not pronounced, which may indicate that a prenuptial molt does occur. The winter plumage of adult males of *nigrifrons* wears to resemble that of the breeding season, but the lack of pronounced abrasion in June specimens suggests that they, too, have an extensive prenuptial molt. In addition, I have examined three male specimens of *nigrifrons* that do show active molt in the spring (one adult and two first-year birds), which proves the existence of this molt but not its frequency.

Females of *coronata* and *auduboni* show various gradations from no prenuptial molt to one as complete as in males. Most show at least a partial replacement of body plumage, usually on the head, back, and breast but averaging less than in males. I have not seen females of *nigrifrons* and *goldmani* in active molt, but the presence of apparently new feathers (in the same area as affected in *coronata* and *auduboni*) suggest that they, too, undergo a partial prenuptial molt.

In the sequence of body plumage and covert replacement there are both differences and similarities among the three molts in the *D. coronata* complex. In the postnuptial and the postjuvenile molts, the sequence of replacement is similar in the marginal and secondary coverts and in the humeral, ventral, and capital tracts. On the other hand, in the postnuptial molt, the spinal, femoral, and caudal (tail coverts) tracts are affected earlier and the crural tract later than in the postjuvenile molt. Most of these differences are slight, but crural and tail covert molt are markedly different, with these areas being affected at reversed and opposite extremes of their cycles. In *Vermivora celata*, Foster (1967) found the sequences of these two molts to be alike. The prenuptial molt in the *Den-*

*droica coronata* complex is more similar in sequence to the postjuvenile molt, although in the former the spinal and ventral tracts precede head molt. In the postjuvenile molt, molt in the humeral and ventral tracts precedes head molt.

In the sequence of molt within individual feather tracts of *Dendroica coronata*, there is an overall similarity among the three molts. In the spinal tract, the prenuptial and postjuvenile molts begin in the anterior pelvic region and move anteriorly and posteriorly. In the prenuptial molt, the pelvic region usually is not affected; instead, replacement begins in the dorsal and interscapular region and moves anteriorly. In the ventral tract, all three molts begin in the sternal region, closely followed (simultaneously in the prenuptial) by the cervical region and then the submalar and/or interramal regions. Molt then moves outward from these loci, and the abdominal area is molted last (this area is usually not affected in the prenuptial molt). In the postjuvenile and prenuptial molts, the capital tract usually begins molt on the foreparts of the head and progresses posteriorly toward a secondary locus on the crown. In the postnuptial molt, the secondary locus is on the forehead, and the primary one is on the crown.

#### Comparison of Molts with *Vermivora celata*

As indicated earlier, only the Orange-crowned Warbler has been studied in sufficient detail (Foster, 1967) to offer good comparison in its molts to those of the *Dendroica coronata* complex. In *V. celata* the postjuvenile molt may begin in any or all of three loci, that is, the spinal, ventral, or alar tracts (marginal coverts). *D. coronata* begins molting in the marginal coverts, whereas molt in the ventral tract occurs in the second stage and in the spinal tract in the third. The second stage of molt in *V. celata* involves the caudal tract, in addition to the three tracts already mentioned; in *D. coronata*, caudal molt (tail coverts) occurs in the last stage. The third stage of molt in *V. celata* involves all tracts, with the addition of molt in the crural and capital tracts. In *D. coronata*, the capital tract is affected earlier, usually half-way through the molt cycle and before caudal molt begins; molt usually begins in the crural tract in the initial stage. Within tracts, the sequence of molts is generally similar between the two species, although there are a few differences. For example, the spinal and ventral molts begin more posteriorly in *D. coronata* than in *V. celata*, usually in the pelvic and sternal regions, respectively, in *D. coronata*. In the capital tract, the molt of *D. coronata* also appears to differ, mainly in that the malar and loreal regions are involved earlier than in *V. celata*.

The postjuvenile molt of *V. celata* appears to be more telescoped than that of the *D. coronata* complex, with a less clearcut distinction between the inception of feather replacement in different tracts and regions. This accounts for many of the differences in the molts between the two species, although there remain those involving early or late extremes in the molt cycle. Thus, in *D. coronata* there is early molt in the crural tract and late molt in the caudal tract, compared to the reverse in *V. celata*. The difference in caudal molt may be related to the

fact that some *V. celata* replace one or more pairs of rectrices, but the significance of delayed crural molt is not apparent.

The postnuptial molt of *V. celata* follows the same sequence in the nonflight feathers as its postjuvenile molt, and it begins after the partial replacement of primary 1+2 (Foster, 1967). This molt differs from the postnuptial molt of *D. coronata* less than it does from the latter's postjuvenile molt, and again the differences stem mainly from the telescoped sequence of *V. celata*. Basically, the differences are that molt in the ventral tract and the greater coverts is comparatively retarded in *D. coronata*, whereas humeral molt is slightly advanced. In the timing of crural and tail covert molt, the postnuptial molt of *D. coronata* agrees with *V. celata*, that is, the caudal molt coming earlier and the crural molt later in the sequence; in the postjuvenile molt of *D. coronata* this sequence is reversed. In molt of the flight feathers, the sequence is identical in the two species in the remiges and similar in the more variably molted rectrices. Loss of the earliest secondary (the ninth) usually coincides with the loss of the fifth primary in *D. coronata* and usually occurs between the loss of the fourth and fifth in *V. celata*.

#### ACKNOWLEDGMENTS

First, I am grateful to the many people involved in my use of specimens from the following institutional and private collections: American Museum of Natural History; University of Alberta; University of Arizona; D. Boag; Provincial Museum of British Columbia; British Museum (Natural History); University of California at Los Angeles (Dickey Collection); California Academy of Sciences; National Museum of Canada; Carnegie Museum of Natural History; Field Museum of Natural History; Denver Natural History Museum; University of Kansas Museum of Natural History; Los Angeles County Museum; Louisiana State University Museum of Natural History; University of Michigan Biological Station; University of Michigan Museum of Zoology; Museum of Comparative Zoology; Museum of Vertebrate Zoology; University of New Mexico; New Mexico State University; Occidental College (Moore Collection); Ohio State University; Royal Ontario Museum; University of Oregon; O. S. Pettingill, Jr.; R. Sale; San Diego Natural History Museum; G. M. Sutton; United States National Museum of Natural History; University of Utah; Virginia Polytechnic Institute and State University (Bailey-Law Collection); and University of Washington. Individual contributions of many are also appreciated, including those of J. Barlow, N. L. Ford, S. D. MacDonald, G. G. Musser, and R. W. Storer. Mercedes Foster, David M. Niles, Kenneth C. Parkes, and Ralph J. Raitt read and commented on earlier drafts of this paper. I am grateful for financial aid from the Chapman Fund and the National Science Foundation and to officials in Canada, Mexico, and the United States for collecting permits. Final thanks go to my wife Claudia, who helped bring this study to its conclusion.



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